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Variation in the local population dynamics of the short-lived *Opuntia macrorhiza* (Cactaceae)

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Variation in the local population dynamics of the short-lived

Opuntia macrorhiza (Cactaceae)

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Running head: Population Dynamics of *Opuntia macrorhiza*
(Cactaceae)

ABSTRACT: Spatio-temporal variation in demographic rates can have profound effects for population persistence, especially for dispersal-limited species living in fragmented landscapes. Long-term studies of plants in such habitats help with understanding the impacts of fragmentation on population persistence but such studies are rare. In this work we reanalyzed demographic data from seven years of the short-lived cactus *Opuntia macrorhiza* var. *macrorhiza* at five plots in Boulder, Colorado. Previous work combining data from all years and all plots predicted a stable population (deterministic $\log \lambda \approx 0$). This approach assumed that all five plots were part of a single population. Since the plots were located in a suburban/agricultural interface separated by highways, grazing lands and other barriers, and *O. macrorhiza* is likely dispersal-limited we analyzed the dynamics of each plot separately using stochastic matrix models assuming each plot represented a separate population. We found that the stochastic population growth rate $\log \lambda_s$ varied widely between populations ($\log \lambda_s = 0.1497, 0.0774, -0.0230, -0.2576, -0.4989$). The three populations with the highest growth rates were located close together in space, while the two most isolated populations had the lowest growth rates suggesting that dispersal between populations is critical for the population viability of *O. macrorhiza*. With one exception, both our prospective (stochastic elasticity) and retrospective (stochastic life table response experiments) analysis suggested that means of stasis and growth, especially of smaller plants, were most important for population growth rate. This is surprising because recruitment is typically the most important vital rate in a short lived species such as *O. macrorhiza*. We found that elasticity to the variance was mostly negligible, suggesting *O. macrorhiza* populations are buffered against large temporal variation. Finally, single-year elasticities to means of transitions to the smallest stage (mostly due to reproduction) and growth differed considerably from their long-term elasticities. It is important to be aware of this difference when using models to predict

the effect of manipulating plant vital rates within the time frame of typical plant demographic studies.

Key Words: *Opuntia macrorhiza*, spatio-temporal variation, fragmented landscape, dispersal, population growth, stochastic elasticity, stochastic LTRE, metapopulation,

Introduction

Spatial and temporal variation in demographic rates can have important consequences for life-history evolution and species persistence (Miller et al. 2011; Villellas et al. 2013). While the relevance of environmental variation is widely appreciated (Boyce et al. 2006), quantifying effects of this variation on population dynamics at local scales requires long-term studies at replicated sites. Many demographic studies, especially in plants, often combine data from different plots (Crone et al. 2011). This spatial averaging can mask important local variation and can lead to incorrect conclusions about the fate of individual populations. Even at relatively small spatial scales populations can show varying dynamics due to alteration of the landscape over time, making local habitat and environmental conditions important (Bock and Bock 1998; Clark 2010). The role of local variation in biotic and abiotic factors on population dynamics is well documented (Davison et al. 2010; Eckberg et al. 2012) suggesting that an analysis of individual populations might be necessary for a better understanding of population dynamics.

Effects of environmental variation on individual populations have been studied using stochastic stage-specific models that yield an estimate of the long-term stochastic growth rate, $\log \lambda_S$ (Caswell 2001). When populations vary in their stochastic growth rates it is natural to ask which vital rates (survival, growth, reproduction) contributed most to the observed spatial variation. This retrospective analysis, known as stochastic life table response experiments (SLTRE; Davison et al. 2010), separates the contributions of means of vital rates from their annual variation to differences in stochastic growth rates. While SLTRE provides information on past effects of vital rates on population dynamics, understanding the fitness consequences of changing vital rates on population growth requires a prospective analysis that quantifies the impacts of changes in vital rates on the stochastic growth rate (Tuljapurkar et al. 2003).

Stochastic elasticities quantify the selection pressure on vital rates (Charlesworth 1999) and help in devising management strategies that target vital rates having major impacts on the stochastic growth rate (Morris and Doak 2002). Elasticity analysis of λ_S assumes that the population has reached the stable stage distribution (SSD) where the proportion of individuals in each stage no longer changes with time and the population grows at a constant rate (demographic equilibrium). However, the response of λ_S to short-term changes in vital rates can substantially differ from that predicted by the elasticity analysis, especially when a population is away from its SSD (Haridas and Tuljapurkar 2007). Knowledge of short-term responses, as quantified by short-term elasticities (Chirakkal and Gerber 2010), is particularly useful since conservation and management efforts typically operate on short time scales (e.g., 10-15 years, Fefferman and Reed 2006).

This study focuses on the population dynamics of the short-lived cactus species *Opuntia macrorhiza* var. *macrorhiza*, (the western prickly pear: average life-span \approx 3 years; Keeler and Tenhumberg 2011) and explores implications for its long-term persistence. Demographic studies of cacti, especially of short-lived cacti, are relatively rare despite their species richness (\approx 1,500 species; Godínez-Álvarez et al. 2003) and their usefulness in understanding the effects of environmental variation on population dynamics (Nobel 2003). We quantified spatio-temporal variation in the population dynamics of *Opuntia macrorhiza* var. *macrorhiza* using demographic data collected over seven years from five plots in Boulder County, Colorado, USA. In previous work, Keeler & Tenhumberg (2011) combined data from all years and all the plots and used a deterministic analysis to estimate population growth rate. By averaging data from different plots, the five populations were treated as replicates because historically the populations were part of a large connected prairie. However, over the last 100 years the landscape became increasingly

fragmented as a result of rapid suburbanization and agricultural use (Bock and Bock 1998). The plots, which vary in grazing, soil and topographical features, are now separated by highways, grazing lands and other barriers potentially limiting dispersal among them (Bennet et al. 1997). If population dynamics differ significantly between plots, population viability might be better assessed by using a metapopulation model (Hanski 1999), which would require information and data on dispersal among populations. Our study had three main objectives: First, we determined the spatio-temporal variation in vital rates and long-term stochastic population growth rates across the five plots. Second, we quantified the contributions of different vital rates to the observed differences in stochastic growth rates, and third, we identified vital rates that are most important for future population viability by evaluating short- and long-term stochastic elasticities of λ_S .

Materials and Methods

Demographic data: *O. macrorhiza* is common to the plains, the Rocky Mountain foothills, and the Great Basin of the United States ranging southward into northern Mexico (Benson, 1992). It is endangered in Iowa, salvage-restricted in Arizona (<http://plants.usda.gov>) and is listed as a species of special concern in Minnesota (<http://www.dnr.state.mn.us>). *Opuntia* spp. is of major economic value in Mexico and recent studies have demonstrated potential use of cactus pear fruit and vegetative cladodes in the development of food and medicine (Feugang et al. 2006). We used monitoring data from five plots of *O. macrorhiza* populations that were collected over seven years (1999-2005; see Fig. A1, Appendix A). These plots were part of a grassland biodiversity study consisting of 68 plots (Bennet et al. 1997) in the Open Space around Boulder, Colorado; for comparison with the previous study of Keeler and Tenhumberg (2011),

we used the same plot numbers. Once part of a large connected prairie, but not so for the past 100 years, the plots are now fragmented with rapid suburbanization and agricultural use. All of the plots are at least 1.6 kilometers apart; with the possible exception of plots 28 and 57 (see Fig. A1, Appendix A). Plot 57 is in a grazing enclosure situated more than 50 m. down and 1 km south of plot 28 which is in the Open Space adjacent to a housing development. The high rising area (more than 100 feet) between plots 57 and 28 is privately owned cattle range limiting movement of people and cows between the sites and thus limiting plant dispersal between the sites. Further, highways and other barriers separate most of the plots. Soil, grazing and topographical characteristics of the plots are summarized in Table B2 of Appendix B. Three plots (28, 57, and 61) were flat with gravelly soil. One plot (52) had similar soil but was on a hilltop (Davidson Mesa). The fifth plot (102), in Chataqua Park Meadow, was on a grass-covered east-facing slope. Two plots (28 and 61) were grazed by cattle in summer, one plot (52) was grazed in winter, and two plots (57 and 102) were not grazed. All plots were 100 m² except one (57), which was 92 m² and had the highest density and absolute number of plants (Keeler & Tenhumberg 2011). Plant sizes were estimated by counting the number of cladodes (flattened shoots or green stems) on each plant in each year. Death of a plant was characterized by the observation of a badly damaged white cladode where a plant was recorded in the previous year. Plants that were entirely yellow were conservatively recorded as present and alive. We made only one survey/plot/year, to count the number of developing fruits. Whenever a plant subdivided, we considered the central ramet the original plant and any peripheral clones were recorded as vegetative reproduction so that new recruits occasionally possessed several cladodes (usually 2-7 cladodes).

Stage structured population model: For each site and year we constructed transition

matrices quantifying the probability of plants of different sizes to change to any possible size in the following years. Following Keeler & Tenhumberg (2011) we grouped *Opuntia* plants into five size classes: plants with 1, 2-3, 4-7, 8-15, and > 15 cladodes and these are labeled here as plants in stages I, II, III, IV and V respectively (see life cycle graph Fig. B1, Appendix B). Though the average lifespan is approximately three years, some individuals can live up to 2 decades (16% and 5% percent of the observed plants in all plots belonged to stages IV and V, respectively; Keeler and Tenhumberg 2011). Plants in stage I were mostly new recruits though a few of them (< 6% in plots 28, 52, 57 and 61) resulted from shrinkage of larger plants. The transition rate between any two stages is estimated from the fates of tagged plants (i.e. stages of the plants) in successive years as well as the size of a new recruit appearing in a given year. In a few cases (see Table B1, Appendix B) the origin of recruits (i.e., the size of parent plant) was unknown. We assumed that these recruits originated from parents whose size distribution was known from information on recruits with known parents. For plants for which information on the number of cladodes was missing (see Table B1, in Appendix B), we assigned the mode of the number of cladodes of plants with known sizes in that year. The choice of mode produced the best initial fit with the observed population counts in all the plots. For plots 52 and 57 we used population data from six annual transition periods, from 1999-2000 to 2004-2005. For the remaining plots (plots 28, 61 and 102) we used data only from 2000-2001 to 2004-2005 (five annual transition periods), as very few plants were sampled during 1999-2000 in these plots. Plot 102 had the minimum data available as we tracked an average of only 20 plants per year during years 2000 to 2005. Average sample sizes of plants for each plot and estimates of transition matrices for each year are given in Table B1 of Appendix B.

Deterministic and Stochastic growth rates: The deterministic growth rate, $\log \lambda$, was

calculated as the leading eigenvalue of the temporally averaged matrices. The stochastic growth rate was calculated assuming that each annual transition matrix occurred with equal probability (= 1/6 for plots 52 and 57 and = 1/5 for other plots) and that there was no temporal autocorrelation. Stochastic iterations for each plot were carried out for 25,000 time steps and the simulation was repeated 100 times. Then we calculated the long-run stochastic growth rate as $\log \lambda_s = (1/T) \sum_t \log \lambda(t)$, where $\lambda(t) = N(t)/N(t-1)$ is the (annual) population growth rate between years $t-1$ and t , and $T = 25,000$ (we omitted the first 2000 iterations to exclude transient effects). The 95% confidence intervals were calculated as

$\log \lambda_s \pm 1.96 \sqrt{\left(\frac{\text{Var}(\log \lambda(T))}{T} \right)}$ (Heyde & Cohen 1985), where the variance is calculated across the 100 repetitions.

Stochastic elasticities: We calculated long-term stochastic elasticities with respect to means (E_{ij}^μ) and standard deviations (E_{ij}^σ) of vital rates (prospective analysis), using the methods in Tuljapurkar et al. (2003). Elasticity to the mean is the proportional change in λ_s when the mean of the vital rate is increased by a small percentage, without changing its variance. Similarly elasticity to the standard deviation is the proportional change in λ_s when the standard deviation of the vital rate is increased by a small percentage, without changing its mean. In addition, we evaluated single-year elasticities of λ_s , which describe the proportional change in λ_s due to a small proportional increase in a vital rate only in a single year (Chirakkal and Gerber 2010). Single-year elasticities do not account for long-term changes in stage-structure resulting from increase in a vital rate every year. We report elasticities of matrix elements summed within each of four types of life-cycle components (Davison et al. 2010): i) stasis ($i = j$), representing

transition rates of surviving plants that do not change size; ii) growth ($i > j$), representing transition rates of plants that survive and grow to a larger size; iii) shrinkage ($i < j$), representing rates corresponding to surviving plants shrinking to a smaller size and iv) transitions to the smallest stage from other stages (first row elements, $(1, j)$, $j > 1$), denoted by TSS, in a single year. TSS mostly included new recruits though it also had a few plants resulting from shrinkage of larger plants ($< 6\%$ in plots 28, 52, 57 and 61).

Stochastic Life Table Response Experiment (SLTRE): We performed the recently developed SLTRE (Davison et al. 2010) to retrospectively quantify the contributions of differences in the means and variances of vital rates to the observed differences in $\log \lambda_s$ of the five plots. First we constructed a reference population (denoted by R), whose transition matrix in a given annual time period (2000-2001 to 2004-2005) is given by the average of the transition matrices from all five plots for that time period. These five annual transition matrices were used to estimate the stochastic growth rate $\log \lambda_s(R)$ for the reference population. Let $\log \lambda_s(P)$ denote the stochastic growth rate and let $\mu_{ij}(P)$ and $\sigma_{ij}(P)$ denote the mean and standard deviation of vital rate (i, j) of a given plot P (where $P = 52, 57, 28, 61$ and 102). Then the difference in stochastic growth rates between the study plot P and the reference plot R is given by (see equation (1) of Davison et al. 2010),

$$\log \lambda_s(P) - \log \lambda_s(R) = \sum_{ij} (\log \mu_{ij}(P) - \log \mu_{ij}(R)) E_{ij}^{\mu} + \sum_{ij} (\log \sigma_{ij}(P) - \log \sigma_{ij}(R)) E_{ij}^{\sigma}$$

where the elasticities E_{ij}^{μ} and E_{ij}^{σ} are evaluated from the stochastic model obtained from averaging demographic matrices for plots P and R every year. The quantity

$$C_{ij}^{\mu} = \sum_{ij} (\log \mu_{ij}(P) - \log \mu_{ij}(R)) E_{ij}^{\mu}$$

measures the contribution of differences in means of vital

rates (to the differences in stochastic growth rates) while the quantity

$C_{ij}^{\sigma} = \sum_{ij} (\log \sigma_{ij}(P) - \log \sigma_{ij}(R)) E_{ij}^{\sigma}$ measures the contribution of differences in variability of

vital rates. We reported the contributions in terms of the four life-cycle components, viz., stasis, growth, shrinkage, and TSS, representing transitions to the smallest stage (i.e., stage I) due to recruitment and shrinkage.

Results

Spatio-temporal variation in long-term stochastic population growth rates: Our

model predicted positive stochastic growth rates for plots 52 ($\log \lambda_s = 0.0774$; 95% CI = 0.002) and 28 ($\log \lambda_s = 0.1497$; 95% CI = 0.01). Plots 57 ($\log \lambda_s = -0.0230$; 95% CI = 0.003), 61 ($\log \lambda_s = -0.2576$; 95% CI = 0.001), and 102 ($\log \lambda_s = -0.4989$; 95% CI = 0.05) had negative stochastic growth rates indicating declining populations in these plots. The magnitudes of stochastic growth rates were 25% (plot 52) to 65% (plot 28, 102) less than the corresponding deterministic growth rates $\log \lambda$ (calculated as the logarithm of the dominant eigenvalue of the temporally averaged demographic matrix) showing the impacts of environmental stochasticity in all the plots studied. Note that in all plots several vital rates (transitions between size classes) had high coefficients of variation (CV > 1, Table B3, Appendix B), and plots 102 and 28 in particular had high CVs in the majority of vital rates.

Stochastic Life Table Response Experiment (SLTRE): The contribution from

differences in means C^{μ} (Fig. 1a) was generally higher in magnitude than the corresponding contributions from differences in standard deviations, C^{σ} (Fig. 1b). Plots differed significantly in the magnitudes of their mean vital rates contributions: plot 57 had the lowest (in magnitude)

contributions among all plots since it was similar to the reference population while vital rate contributions in plot 28 were the largest followed by plot 102. Means of stasis had the largest impact on the observed differences in stochastic growth rates in two plots (plots 28, 57) while means of growth transitions had the largest impact in the other three plots (plots 52, 61 and 102); contribution from means of TSS was important only in plots 28 and 102 (Fig. 1a). Life-cycle components in plots 28 and 102 which had relatively large C^μ values also had large C^σ values (Fig. 1b) reflecting the high CVs in the majority of the vital rates in these plots (Table B3, Appendix B). Variability in vital rates of plots 52, 57 and 61 had negligible effects on spatial differences in stochastic growth rates.

Stochastic elasticity to the mean (E_{ij}^μ) and standard deviation (E_{ij}^σ): Mean elasticities to the four life cycle components were similar in all plots except for plot 102 where the magnitudes of E_{ij}^μ were much larger (Fig. 2a). In all plots means of stasis had the highest elasticity among vital rates followed by growth (Fig. 2a). Transition to stage I (TSS), which included mostly new recruits, had a relatively small impact on the stochastic growth rate in all plots, except in plot 102. Elasticities to stasis and growth of smaller plants, especially of plants in stage II, were the highest in all plots (Fig. C1, Appendix C). Compared to elasticities to the means described above, elasticities to the standard deviations (E_{ij}^σ) were very small in magnitude in all plots except in plot 102 (Fig. 2b). Values of E_{ij}^σ were negative for most transition rates in all the plots implying that λ_s would decrease when variances of these vital rates are increased.

Comparison of long-term and single-year elasticities: We show the difference between long-term and single-year elasticities in Fig.3. Positive values imply that long-term elasticities exceed short-term elasticities indicating that initially the effect of changing a vital rate

is smaller than that expected based on long-term elasticities. Among the four life cycle components we found that single-year elasticities to means of TSS and growth differed the most from their long-term elasticities in all plots, especially in plots 28, 61 and 102 (Fig. 3a). In these plots (plots 28, 61 and 102) differences between short- and long-term elasticities were also sizable for stasis. The differences between short- and long-term variance elasticities (as measured by E^σ) were generally smaller than the corresponding differences between short- and long-term mean elasticities; we observed substantial differences only in plots 28, 61 and especially in plot 102 (Fig. 3b).

Discussion

We analyzed the spatio-temporal variation in population dynamics of the short-lived cactus, *O. macrorhiza* var. *macrorhiza*, taking advantage of one of very few long-term data sets on plant demography in a fragmented urban environment that has witnessed major changes in the recent past. In the study area only 6% of the vegetation consisted of *O. macrorhiza* (Bennet et al. 1997), and dispersal between monitoring plots was likely uncommon because *O. macrorhiza* recruits are mostly found close to the mother plant with an average dispersal distance of 14cm for vegetative recruits and 63cm for seedlings (Keeler and Tenhumberg 2011). Because of the sparse distribution and low dispersal rates between plots, we evaluated if in this landscape *O. macrorhiza* exhibits a metapopulation structure.

Previous work (Keeler & Tenhumberg 2011) combined demographic data from all seven years and five plots studied here, and concluded that overall the population is stable (i.e., deterministic population growth rate $\log \lambda \approx 0$). In contrast, our models predicted that populations in only two plots will increase annually while populations in the remaining three

plots face extinction. These results seem consistent with a metapopulation framework (Hanski 1999), with plot 28 ($\log \lambda_s = 0.1497$) and 52 ($\log \lambda_s = 0.0774$) serving as source populations and the remaining as sink populations (see map in Appendix A). The farther away the plots were from the source population the lower was the population growth rate. Plot 57 was nearest and hence was predicted to decrease annually by a smaller amount ($\log \lambda_s = -0.0230$). Plot 61 was more isolated from the source populations and its population size was predicted to decline more quickly ($\log \lambda_s = -0.2576$). The most isolated population in plot 102 ($\log \lambda_s = -0.4989$) had the lowest predicted population growth rate and was likely to go extinct in the near future, especially because of its current small population density (19.3 plants/m², Keeler and Tenhumberg 2011). Additional information on dispersal probabilities between populations would be useful to evaluate the persistence probability of the entire metapopulation.

O. macrorhiza is a short lived cactus species with an average life expectancy of 3 years (Keeler and Tenhumberg 2011). Based on studies of other short lived perennial plant species (*Anthyllis vulneraria* in Davison et al. 2010; *Plantago coronopus* Villelas et al 2013), we would expect that differences in mean fertility would make a large contribution to differences in stochastic population growth rates. In contrast, our analysis using the SLTRE showed that, with the exception of plot 102, mean fertility had the smallest contribution to explaining the variation in stochastic growth rates between populations. The high mortality of early stage plants (Keeler and Tenhumberg 2011) in most plots suggests that fertility, in comparison to survival, would contribute less to difference in stochastic growth rates.

Why the population dynamics differ between plots is unclear. For instance, even though the populations in plot 28 and 61 grow both on flat, gravel soil, and are exposed to summer grazing (Appendix A, Table 2), one constitutes a source population (plot 28, $\log \lambda_s = 0.1497$),

and the other a sink population (plot 61, $\log \lambda_s = -0.2576$). Further, our analysis showed that temporal variation in vital rates significantly affected all five populations as evidenced by the differences in stochastic and deterministic growth rates. However, Keeler and Tenhumberg (2011) found no effect of annual precipitation on the population dynamics though there were significant drought years during the study period (1998-2005). Further studies are required to get a better understanding of the underlying mechanisms explaining the spatio-temporal variation in the population dynamics of *O. macrorhiza* in the Boulder Open Space.

To understand what factors are important for future population viability we evaluated stochastic elasticities. With the exception of plot 102, the elasticities of life cycle components were very similar across the five plots. Previous work also observed similar elasticities across five populations of the long-lived perennial, *Silene acaulis* L. (Caryophyllaceae) (Morris and Doak 2005). Similar to the results from SLTRE, reproduction was relatively less important for population growth rate which contrasts with the expectation based on general life-history models for short-lived species (Gaillard et al. 2005). Since *O. macrorhiza* is short-lived we would expect that survival and growth of plants in their early stages is important for *O. macrorhiza* population dynamics. This is confirmed by examining the elasticities of single matrix elements (Figure C1, Appendix C): in all plots transitions from stage II plants (representing their survival growth etc.) are most important for the stochastic growth rate, $\log \lambda_s$. Interestingly, we found large differences between long- and short-term elasticities (Fig. 3). There were significant drought years during the study period (Keeler and Tenhumberg 2011) which could cause these differences by perturbing a population away from a stable stage distribution (SSD; Haridas & Tuljapurkar 2007; Chirakkal and Gerber 2010). In all the plots the observed stage structure in the years of study (1998-2005) showed substantial fluctuations from the SSD calculated from the

temporally averaged demographic matrix (Figs. C2 and C3, Appendix C). Our results contrast with the recent study of Williams et al. (2011) which reported that many plant populations are near their SSD. Note that Williams et al. (2011) did not incorporate temporal variation in vital rates which is substantial in all plots we studied. Being aware of differences between long- and short-term elasticities is important because management strategies usually aim to achieve target population growth rates in short time periods (Chirakkal & Gerber 2010).

In conclusion, our study uses spatio-temporal demographic analysis to reveal a metapopulation structure of *O. macrorhiza* consisting of two source populations (large positive stochastic growth rates), and stochastic growth rates of the other populations decreased with distance from the source populations. Hence, assessing *O. macrorhiza* persistence requires knowledge of dispersal between plots and future work should focus on collecting data on dispersal rates. Further, this study provides an example of a short-lived species where, in contrast to some previous studies, mean stasis and growth, especially of smaller plants, are more important for the stochastic growth rate than mean recruitment rates.

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 402

Supplemental material

Appendix A. Map (Figure A1) of the City Of Boulder Open Space and Mountain Parks (2013) and locations of five plots (numbered 52, 57, 28, 61 and 102) of *Opuntia macrorhiza* var. *macrorhiza* used in the study.

Appendix B. Life cycle graph (Figure B1), annual demographic matrices (Table B1), their temporal averages and coefficients of variation (Table B3). Also shown is the table of soil, grazing and topographical features of the five study plots (Table B2).

Appendix C. Elasticities to means of matrix elements for all the five plots (Figure C1). Observed annual stage frequencies and the Stable Stage Distribution (SSD) for plots 52 and 57 (Figure C2) and plots 28, 61 and 102 (Figure C3) are also shown.

Figure Legends

Figure 1: Results from the SLTRE on the contribution of life cycle components to the observed differences in stochastic growth rates between the five populations. a) Contributions of differences in means (C^μ); b) Contributions of differences in SDs (C^σ). Each bar represents the contribution of matrix elements summed within each of four life-cycle components: i) stasis ($i = j$), representing transition rates of surviving plants that do not change size; ii) growth ($i > j$), representing transition rates of plants that survive and grow to a larger size; iii) shrinkage ($i < j$), representing rates corresponding to surviving plants shrinking to a smaller size and iv) transitions to the smallest stage from other stages (first row elements, $(1, j)$, $j > 1$), denoted by TSS, in a single year. See Figure B1 of Appendix B for the life cycle graph. Also shown are stochastic growth rates $\log \lambda_s$ for each plot.

Figure 2: a). Elasticity E_{ij}^μ to means of life cycle components; b). Elasticity E_{ij}^σ to SDs of life cycle components. Each bar represents elasticity of matrix elements summed within each of four life-cycle components: i) stasis ($i = j$), representing transition rates of surviving plants that do not change size; ii) growth ($i > j$), representing transition rates of plants that survive and grow to a larger size; iii) shrinkage ($i < j$), representing rates corresponding to surviving plants shrinking to a smaller size and iv) transitions to the smallest stage from other stages (first row elements, $(1, j)$, $j > 1$), denoted by TSS, in a single year. See Figure B1 of Appendix B for the life cycle graph.

Figure 3: a) Differences between long-term E^μ elasticities and corresponding single-year

446 elasticities for life cycle components ; b) Differences between long-term E^σ elasticities and
 447 corresponding single-year elasticities for life cycle components. Each bar represents the
 448 difference between long- and single-year elasticity of matrix elements summed within each of
 449 four life-cycle components: i) stasis ($i = j$), representing transition rates of surviving plants that
 450 do not change size; ii) growth ($i > j$), representing transition rates of plants that survive and grow
 451 to a larger size; iii) shrinkage ($i < j$), representing rates corresponding to surviving plants
 452 shrinking to a smaller size and iv) transitions to the smallest stage from other stages (first row
 453 elements, $(1, j), j > 1$), denoted by TSS, in a single year. See Figure B1 of Appendix B for the
 454 life cycle graph.

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Figure 1

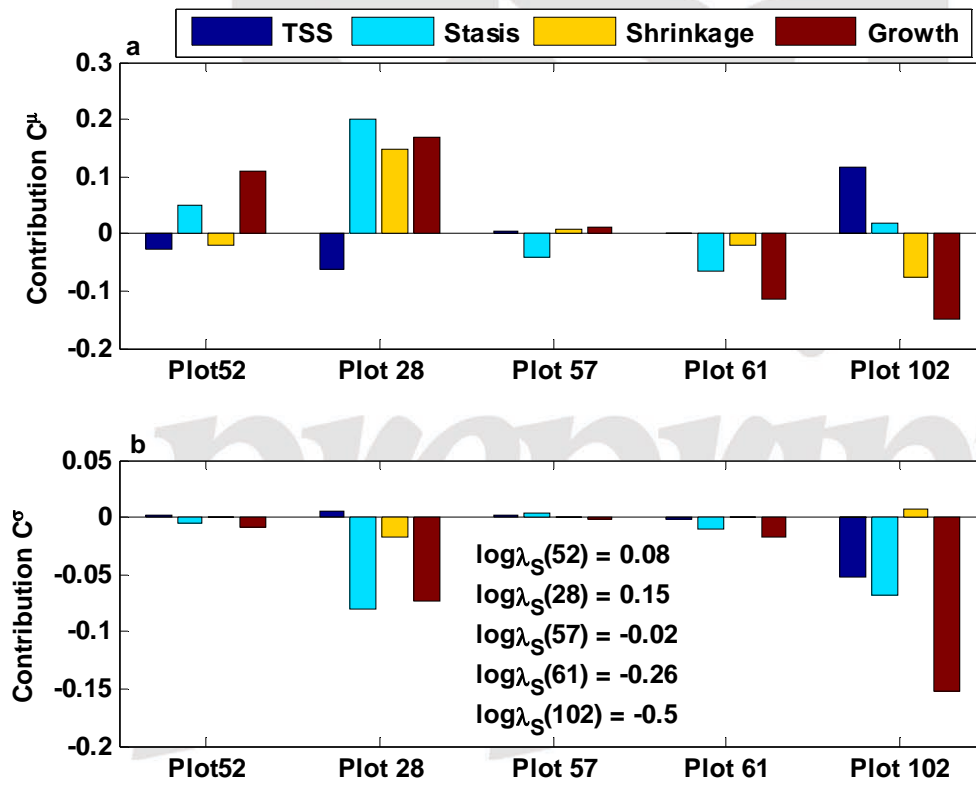


Figure 2

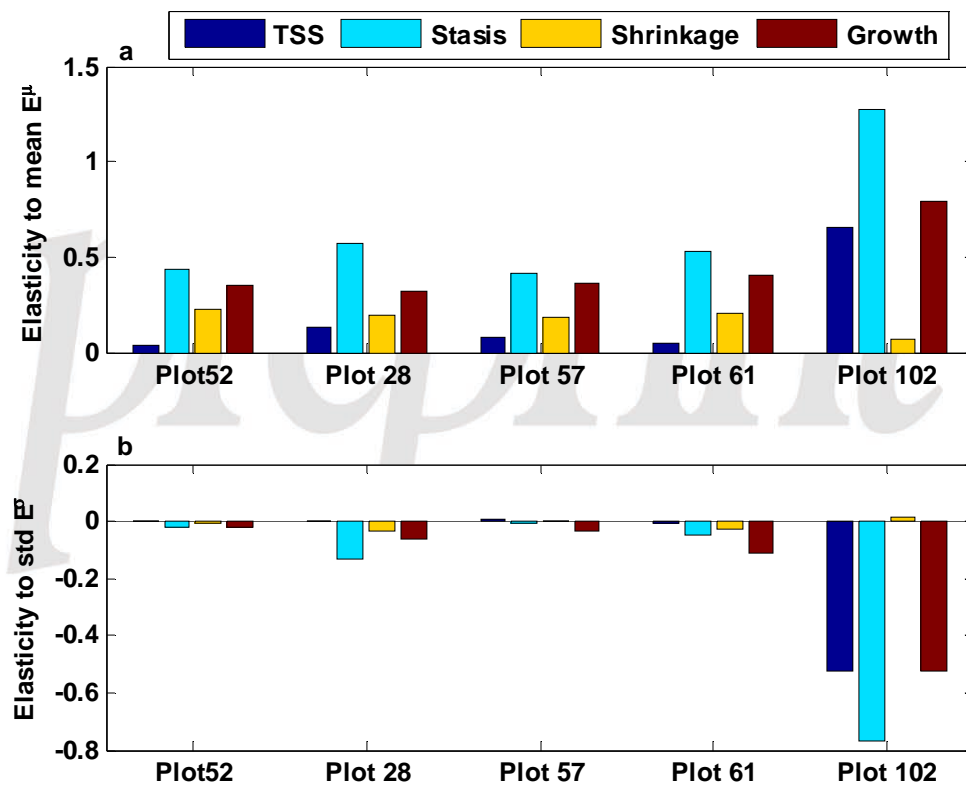


Figure 3

